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Nutrient coordination mechanism of tiger nut induced by rhizosphere soil nutrient variation in an arid area, China

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Abstract: Tiger nut is a bioenergy crop planted in arid areas of northern China to supply oil and adjust the planting structure. However, in the western region of Inner Mongolia Autonomous Region, China, less water resources have resulted in a scarcity of available farmland, which has posed a huge obstacle to planting tiger nut. Cultivation of tiger nut on marginal land can effectively solve this problem. To fully unlock the production potential of tiger nut on marginal land, it is crucial for managers to have comprehensive information on the adaptive mechanism and nutrient requirement of tiger nut in different growth periods. This study aims to explore these key information from the perspective of nutrient coordination strategy of tiger nut in different growth periods and their relationship with rhizosphere soil nutrients. Three fertilization treatments including no fertilization (N:P (nitrogen:phosphorous)=0:0), traditional fertilization (N:P=15:15), and additional N fertilizer (N:P=60:15) were implemented on marginal land in the Dengkou County. Plant and soil samples were collected in three growth periods, including stolon tillering period, tuber expanding period, and tuber mature period. Under no fertilization, there was a significant correlation between N and P contents of tiger nut roots and tubers and the same nutrients in the rhizosphere soil ($P<0.05$). Carbon (C), N, and P contents of roots were significantly higher than those of leaves ($P<0.05$), and the C:N ratio of all organs was higher than those under other treatments before tuber maturity ($P<0.05$). Under traditional fertilization, there was a significant impact on the P content of tiger nut tubers ($P<0.05$). Under additional N fertilizer, the accumulation rate of N and P was faster in stolons than in tubers ($P<0.05$) with lower N:P ratio in stolons during the tuber expansion period ($P<0.05$), but higher N:P ratio in tubers ($P<0.05$). The limited availability of nutrients in the rhizosphere soil prompts tiger nut to increase the C:N ratio, improving N utilization efficiency, and maintaining N:P ratio in tubers. Elevated N levels in the rhizosphere soil decrease the C:N ratio of tiger nut organs and N:P ratio in stolons, promoting rapid stolon growth and shoot production. Supplementary P is necessary during tuber expansion, while a higher proportion of N in fertilizers is crucial for the aboveground biomass production of tiger nut.

Keywords: tiger nut; stoichiometry; rhizosphere soil; nitrogen addition; marginal land

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1 Introduction

The absorption, transport, and allocation of plant nutrient elements can reflect the material and energy cycle within plants. It is of great significance to understand the nutrient limitation of plants,

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implement nutrient management, and predict vegetation dynamics (Ågren and Weih, 2012; Tian et al., 2019). Especially in the arid areas with limited resources, plants have more sensitive physiological processes (Luo et al., 2021). Plants adapt to the harsh environment by increasing the C content of organs to form a more stable structure (Dong et al., 2023), although at the cost of a lower photosynthetic rate, the aboveground part of plants will increase N content to resist drought stress (Wang et al., 2019b), and plants also increase N content of leaves to improve their resource competitiveness (Su et al., 2022). When plant growth is limited by nutrient and water supply under dry conditions, plants may invest relatively more of their assimilated C into their root system, thereby increasing their ability to absorb water and nutrients (He and Djikstra, 2014). These theories provide important guidance for ecological restoration and agricultural production, and plant stoichiometry will still be a research hotspot in the future.

Under the background of global climatic change and food crisis, breeding crops with high adaptability, increasing crop yields, and making full use of marginal lands are of utmost importance (Khanna et al., 2021; Maranna et al., 2021). The complex soil environment in arid areas poses a great challenge to crop managers, and adjusting management measures to achieve production purposes under a limited environment has always been a hot topic (Xue et al., 2019; Hafez et al., 2021). Crop stoichiometry is a very critical branch of plant stoichiometry, and it reveals which nutrients limit crop growth and whether the adaptation strategy of crops is suitable in a limited environment (Sadras, 2006; Yan et al., 2022). Exploring ways to optimize crop management practices from the perspective of the relationship between soil factors and crop stoichiometry is effective (Saleem et al., 2020). In the presence of low N levels in the soil, the C:N ratio of wheat leaves increased to enhance N utilization efficiency, but it could be modified by supplementing N fertilizer to improve the growth of wheat (Wang et al., 2019a). In yellow mud fields, the negative correlation between soil P content and the N:P or C:P ratio of rice revealed that rice growth was limited by P, while N supply was abundant, so supplementing P fertilizer emerged as a viable solution to meet P demands of rice (Wang et al., 2017). A N:P ratio of <4.0 in maize grains was associated with lower yields, but increasing the application of N fertilizer can help mitigate the risk of yield decline (Ma et al., 2016). Overall, a comprehensive understanding of stoichiometric changes during crop growth and their relationship with soil nutrients provides valuable information for management, which is very meaningful for improving management measures.

Tiger nut (*Cyperus esculentus* L. var. *sativus* Boeck) is a highly versatile tuber crop with a high-quality oil crop and contains many kinds of active substances, more and more attention has been paid to its health and nutritional value recently (Zhang et al., 2022a). Tiger nut has been widely planted for food purposes in many countries in Europe and Africa (Bezerra et al., 2023). It has been proven not only to resist extreme environment, but also to thrive in marginal or desert fringe lands (Tumbleson and Kommedahl, 1961; Stoller, 1973; Wilen et al., 1996; Yang et al., 2022). In recent years, tiger nut has been vigorously promoted in arid areas of northern China to adjust the planting structure (Liu et al., 2022; Tan et al., 2022a). However, the available arable land in China has nearly reached its peak, and the promotion of tiger nut has been hindered, so the marginal land with production potential has become an important basis for expanding the cultivation of tiger nut and alleviating the pressure of insufficient arable land (Kuang et al., 2022; Wang et al., 2022).

Recent research on tiger nut has primarily focused on variations in tuber yield, as well as the aboveground and underground biomasses, under single or mixed fertilization method (Li et al., 2004; Pascual-Seva et al., 2009; Wang et al., 2022; Cao et al., 2023). While significant progress has been made in this area, there is still potential to further explore the production capability of tiger nut. Obtaining a clearer understanding of the nutrient requirements of tiger nut in different growth periods becomes particularly important, especially when cultivating them on marginal land that require precise management measures. Moreover, previous studies have primarily examined certain physiological traits of tiger nut, predominantly focused on the tuber, while neglecting the nutritional coordination strategies among various organs (Zhang et al., 2022b; Li et

al., 2023). Therefore, this study aims to reveal the nutritional coordination mechanisms of tiger nut on marginal land and explore the nutrient requirements of tiger nut in different growth periods, by considering the stoichiometric characteristics of different organs during various growth stages and their relationship with nutrient content of the rhizosphere soil.

2 Materials and methods

2.1 Study area

This study was conducted in a marginal land in the Dengkou County, Inner Mongolia Autonomous Region, China (40°27'32"N, 106°33'28"N; Fig. 1). The range of average annual precipitation was 33.3–199.0 mm, but the average annual evaporation is more than 2000.0 mm. The annual average temperature was 7.8°C, with the maximum of 39.0°C. The frost period was 195–245 d. The northwest wind was strong in winter, with the maximum of 12.0 m/s. The soil is aeolian soil, the particles less than 50 μm account for 6.26%, and less than 200 μm account for 47.14%. Natural vegetation in the study area included *Agriophyllum squarrosum* (L.) Moq., *Suaeda glauca* (Bunge) Bunge, *Nitraria tangutorum* Bobr., etc.

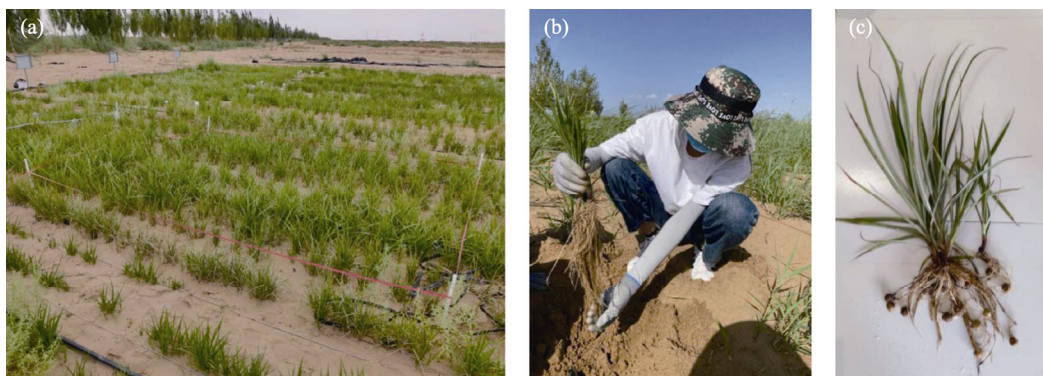


Fig. 1 Tiger nut planting (a) in the Dengkou County, Inner Mongolia Autonomous Region, China, sampling (b), and mature plant (c)

2.2 Field experiment

The experiment was conducted on 25 June, 2022 and a harvest time of 20 October, 2022. Three plots, each measuring 30 m×20 m in size, were utilized for planting. The planting density of tiger nut was set at 30 cm×20 cm, with two tiger nut seeds placed in each hole. This resulted in approximately 30 tiger nut seeds being used per square meter. The seeds were planted at a depth of 4–5 cm.

A drip irrigation method was employed in all three plots. It was carried out twice a week, with a minimum interval of 2 d between each session. A total of 2400 m³/hm² of water quota was applied via drip irrigation in each plot.

Three different fertilization management methods were implemented in three plots for this study (Fig. 2). All fertilization was conducted simultaneously with tiger nut sowing, without any subsequent top dressing, and only inorganic fertilizers (RC(O)NH₂ and P₂O₅) were used. The first treatment involved no fertilization (N:P=0:0). The purpose of this treatment was to investigate the nutrient coordination mechanism of tiger nut in marginal land with limited resources. The second treatment involved traditional fertilization (N:P=15:15). In this case, N fertilizer was applied with an amount of 150 kg/hm², and P fertilizer with an amount of 150 kg/hm². The aim was to examine the nutrient coordination mechanism of tiger nut under the same management practice as traditional crops in marginal land. The third treatment involved additional N fertilizer (N:P=60:15). We applied N fertilizer with an amount of 600 kg/hm² and P fertilizer with an

amount of 150 kg/hm^2 . The design of this approach is built upon the findings of our previous study conducted in 2021, which revealed a significant response of tiger nut spatial distribution to N (Tan et al., 2022b). Numerous studies have also illustrated the impact of N addition on tuber crop yields (Nyawade et al., 2020; Li et al., 2021; Yang et al., 2021). Thus, we hypothesize that a substantial increase in N content may influence the nutritional coordination pattern of tiger nut reproductive organs, consequently influencing the shoot production from tiger nut stolons.

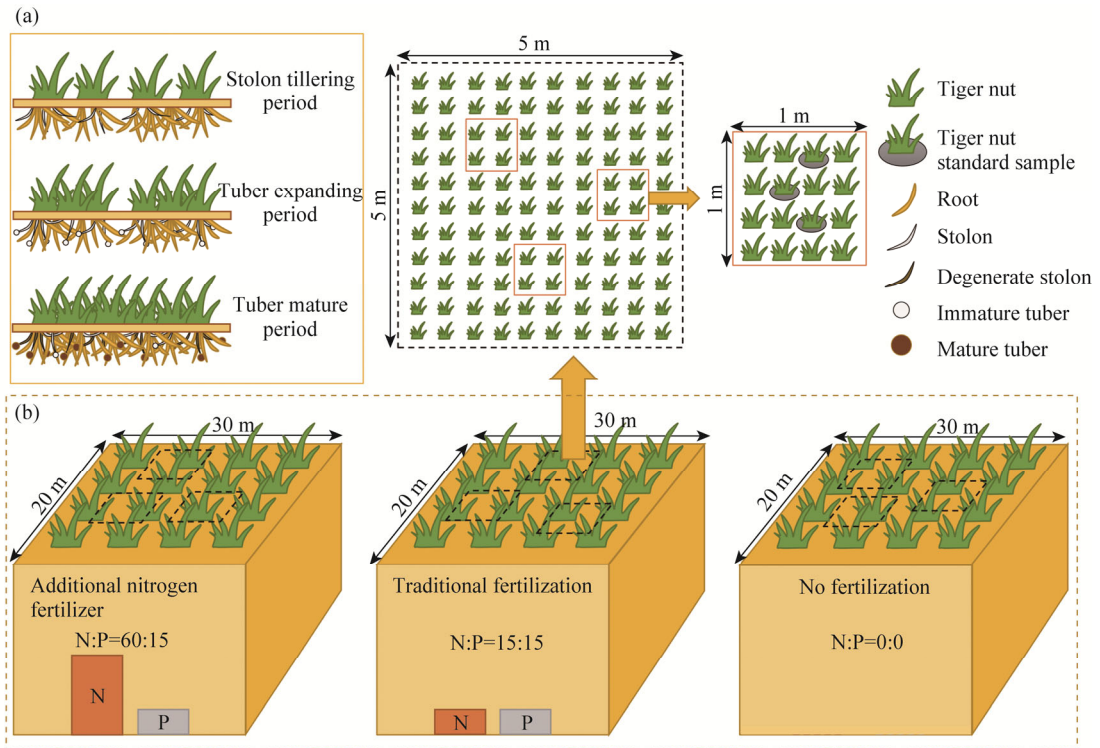


Fig. 2 Planting preparation, investigated periods, sampling method (a), and three treatments (b). Three 5 m×5 m quadrats were randomly set in each treatment, then three 1 m×1 m plots were randomly set in each quadrat. N, nitrogen; P, phosphorus.

2.3 Investigation period

Three crucial growth periods of tiger nut were chosen to reflect their adaptation process in a limited environment (Follak et al., 2016; Tan et al., 2022b). The investigation periods encompassed the stolon tillering period (STP), characterized by the production of stolons; the tuber expanding period (TEP), marked by the development of immature white tubers; and the tuber mature period (TMP), in which the tubers turn red or brown (Fig. 2).

2.4 Tiger nut and soil sample collection

Three 5 m×5 m quadrats were randomly set in each treatment, and within each quadrat, three 1 m×1 m plots were randomly set (Fig. 2). In each period, the height and width of tiger nut in the 1 m×1 m plot were measured first. Then, three standard tiger nut plants with similar height and width were collected (Fig. 2). When collecting, we used a shovel to dig out the entire plant, ensuring that the excavation range was as large as possible to prevent damage to the root. The rhizosphere soil utilized in this study was defined as soil situated within the 2-mm of the root surface. The roots were gingerly shaken to dislodge any extraneous soil clumps, with the rhizosphere soil subsequently procured via deliberate brushing of the remaining soil (DeAngelis et al., 2009; Ren et al., 2020). And tiger nut samples were subsequently placed in plastic bags for

further testing.

2.5 Determination of tiger nut chemical properties and soil properties

The organs of tiger nuts can be classified into vegetative organs and reproductive organs. Vegetative organs include leaf and root, while reproductive organs include stolon and tuber (Tan et al., 2022b). We separate four different organs of tiger nut and dry them at 70°C for 72 h. After grinding, we determined the C content of these tissues by potassium dichromate outer heating, including leaf carbon content (LCC), root carbon content (RCC), stolon carbon content (SCC), and tuber carbon content (TCC). The N and P contents of these tissues were determined by an automatic chemical analyzer (Smartchem 450, AMS Alliance, Rome, Italy) after catalytically boiled, including leaf nitrogen content (LNC), root nitrogen content (RNC), stolon nitrogen content (SNC), tuber nitrogen content (TNC), leaf phosphorus content (LPC), root phosphorus content (RPC), stolon phosphorus content (SPC), and tuber phosphorus content (TPC).

After passing each soil sample through a 0.25-mm sieve, we extracted the soil samples by KCl or NaHCO₃ to determine available nitrogen in rhizosphere soil (ANR) or available phosphorus in rhizosphere soil (APR), total nitrogen in rhizosphere soil (TNR), and total phosphorus in rhizosphere soil (TPR) by Smartchem 450 analyzer. The organic matter in rhizosphere soil (OMR) was determined by potassium dichromate dilution calorimetry.

2.6 Data analysis

T-test was used to analyze the differences in the element content of tiger nut or soil nutrient under different treatments and periods. The allometric growth equation was used to analyze the allocation of nutrient elements during growth process of tiger nuts (Zhang et al., 2020). Pearson correlation analysis was used to analyze the correlation between soil nutrients and nutrient elements of tiger nuts. Redundancy analysis (RDA) was used to identify the main types of soil nutrients causing differences in nutrient elements of tiger nuts under different treatments. These analyses were completed by R software v.4.2.2.

3 Results

3.1 Growth performance of tiger nut

After tuber production, average plant height and crown width of tiger nut were significantly higher under additional N fertilizer than under the other two treatments. However, there were no significant differences between the other two treatments (Table 1).

In STP, there were no significant differences in the dry biomass of each organ of tiger nut among the three treatments. Meanwhile, in TEP, there was a significant difference in the average tuber dry biomass of tiger nut among the three treatments. Notably, the highest tuber dry biomass was observed under no fertilization, while the lowest was recorded under additional N fertilizer. In TMP, the average stolon dry biomass of tiger nut was significantly higher under additional N fertilizer than under the other two treatments. However, the average tuber dry biomass of tiger nut remained significantly lower under additional N fertilizer than under the other two treatments. But under traditional fertilization, the average tuber dry biomass of tiger nut exceeded that under no fertilization in TMP. Lastly, the number of tiger nut per square meter was the highest under additional N fertilizer, and the lowest under no fertilization. These differences among the three treatments were significant (Table 1).

3.2 Allocation of nutrient elements in tiger nut

As tiger nut grew, LCC and RCC decreased under all fertilization treatments. In TMP, SCC increased significantly under additional N fertilizer and was higher than those of other two treatments. TCC reached its highest point in TEP under no fertilization, however, there was no significant difference in the TCC between no fertilization and traditional fertilization in TMP, and both were significantly higher than that under additional N fertilizer (Fig. 3).

Table 1 Growth performance of tiger nut under different growth periods and treatments

Parameter	Growth period	Additional N fertilizer	Traditional fertilization	No fertilization
Average plant height (cm)	STP	30.81±6.75 ^a	31.67±7.33 ^a	32.19±10.52 ^a
	TEP	43.04±6.97 ^a	37.41±4.36 ^b	33.74±9.11 ^b
	TMP	34.93±7.41 ^a	29.00±5.76 ^b	27.78±5.32 ^b
Average crown width per plant (cm)	STP	26.48±8.75 ^a	28.63±9.09 ^a	29.33±10.39 ^a
	TEP	37.74±6.91 ^a	33.70±10.74 ^a	30.93±10.73 ^b
	TMP	36.74±8.35 ^a	32.04±8.68 ^b	28.33±6.27 ^b
Average dry biomass of leaf per plant (g)	STP	1.76±0.93 ^a	1.84±1.04 ^a	1.71±1.21 ^a
	TEP	3.05±0.83 ^a	2.76±0.83 ^a	2.67±1.19 ^a
	TMP	1.66±0.60 ^a	1.34±0.53 ^b	1.15±0.53 ^b
Average dry biomass of root per plant (g)	STP	0.63±0.39 ^a	0.57±0.32 ^a	0.63±0.33 ^a
	TEP	1.06±0.74 ^a	1.19±0.77 ^a	1.12±0.63 ^a
	TMP	0.81±0.28 ^a	0.74±0.30 ^{ab}	0.61±0.24 ^b
Average dry biomass of stolon per plant (g)	STP	0.049±0.039 ^a	0.040±0.020 ^a	0.049±0.044 ^a
	TEP	0.089±0.040 ^a	0.103±0.049 ^a	0.096±0.041 ^a
	TMP	0.060±0.036 ^a	0.043±0.016 ^b	0.044±0.029 ^b
Average dry biomass of tuber per plant (g)	TEP	0.74±0.28 ^c	0.98±0.56 ^b	1.51±0.99 ^a
	TMP	1.31±0.39 ^c	2.69±1.38 ^a	2.12±1.15 ^b
Number of tiger nuts per square meter	TMP	144.56±21.29 ^a	120.11±23.85 ^b	10.33±2.35 ^c

Note: Different lowercase letters within the same parameter indicate significant difference among different growth periods. STP, stolon tillering period; TEP, tuber expanding period; TMP, tuber mature period (TMP). Mean±SE.

LNC, RNC, and SNC also decreased with the growth of tiger nut. Traditional fertilization significantly increased LNC and SNC, while the addition of N provided an additional increase in LNC and SNC. TNC increased significantly with the growth of tiger nut under fertilization treatment, but the tubers under traditional fertilization accumulated more N compared with additional N fertilizer (Fig. 3).

Fertilization treatment significantly increased P content in leaf and root compared with no fertilization. SPC increased with the growth of tiger nut under additional N fertilizer but decreased under the other treatments, and SPC under additional N fertilizer was significantly higher than that under the other treatments. TPC significantly increased with the growth of tiger nut, and the tubers under traditional fertilization accumulated the highest amount of P (Fig. 3).

3.3 Allometric relationship of nutrient elements among different organs of tiger nut

Under no fertilization, the increase rate of nutrients in tubers was almost faster than that in stolons in TEP. However, in TMP, this phenomenon only occurs with P content (Fig. 4). Under traditional fertilization, the rate of nutrient increase in both tuber and stolon was almost the same (Fig. 4). Under additional N fertilizer, the increase rate of SNC was faster than that of TNC in TEP, but their increase rate remained consistent in TMP. Similarly, P also showed a faster increase rate in stolon compared with tuber under additional N fertilizer (Fig. 4).

Under no fertilization, the rate of increase in nutrients in tuber was almost faster than that in stolon in TEP. However, in TMP, this phenomenon only occurred with P content (Fig. 5). Under traditional fertilization, the rate of nutrient increase in both tuber and stolon was almost the same (Fig. 5). Under additional N fertilizer, the rate of increase in SNC was faster than that of TNC in TEP, but their increase rate remained consistent in TMP. P content showed a faster rate of increase in stolon compared with tuber under additional N fertilizer.

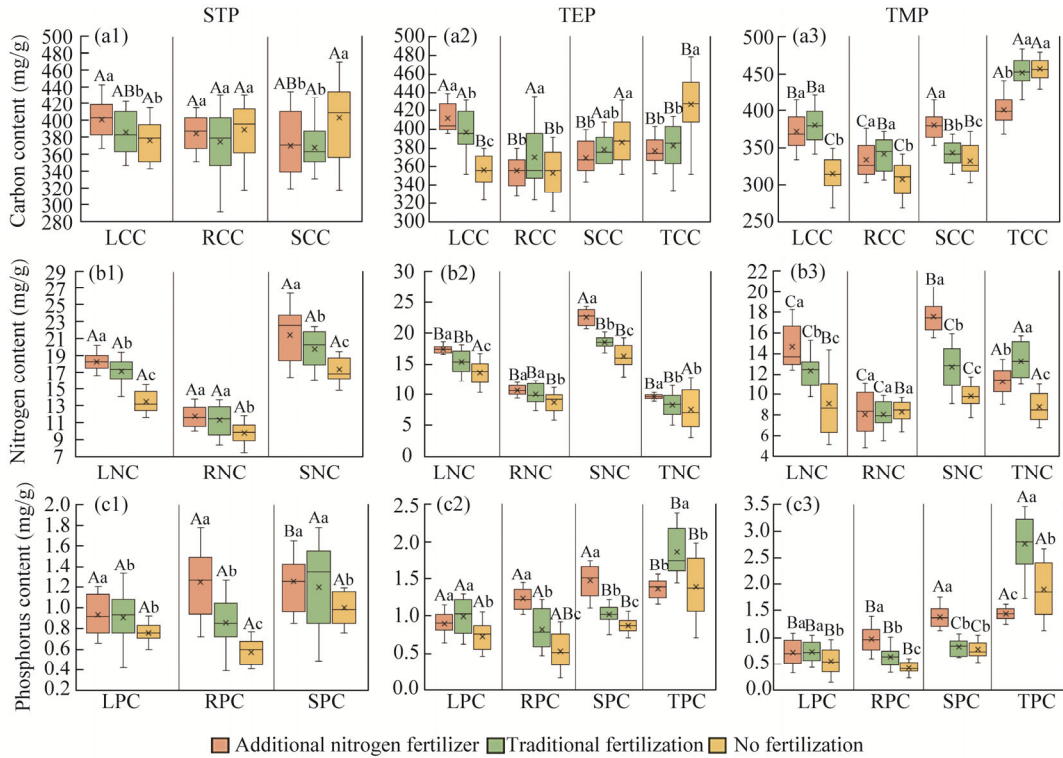


Fig. 3 Carbon (a1–a3), nitrogen (b1–b3), and phosphorus (c1–c3) contents in tiger nut organs under different growth periods and treatments. Different uppercase letters within the same treatment indicate significant differences among different periods at $P < 0.05$ level, while different lowercase letters within the same period indicate significant differences among different treatments at $P < 0.05$ level. Boxes indicate the IQR (interquartile range, 75th to 25th of the data). The median value is shown as a line within the box. Cross symbol is shown as mean. Lines extend to the most extreme value within $1.5 \times \text{IQR}$. Signs are the same in Figures 6 and 7. LCC, leaf carbon content; RCC, root carbon content; SCC, stolon carbon content; TCC, tuber carbon content; LNC, leaf nitrogen content; RNC, root nitrogen content; SNC, stolon nitrogen content; TNC, tuber nitrogen content; LPC, leaf phosphorus content; RPC, root phosphorus content; SPC, stolon phosphorus content; TPC, tuber phosphorus content; STP, stolon tillering period; TEP, tuber expanding period; TMP, tuber mature period.

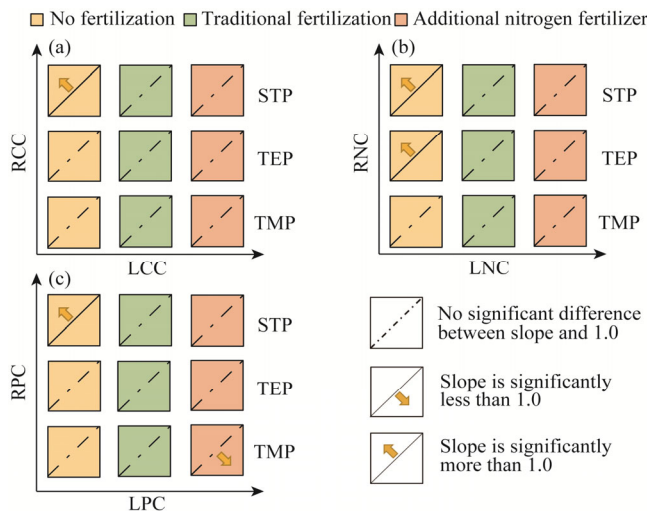


Fig. 4 Allometric relationship of nutrient element contents between leaf and root. (a), relationship between LCC (leaf carbon content) and RCC (root carbon content); (b), relationship between LNC (leaf nitrogen content) and RNC (root nitrogen content); (c), relationship between LPC (leaf phosphorus content) and RPC (root phosphorus content).

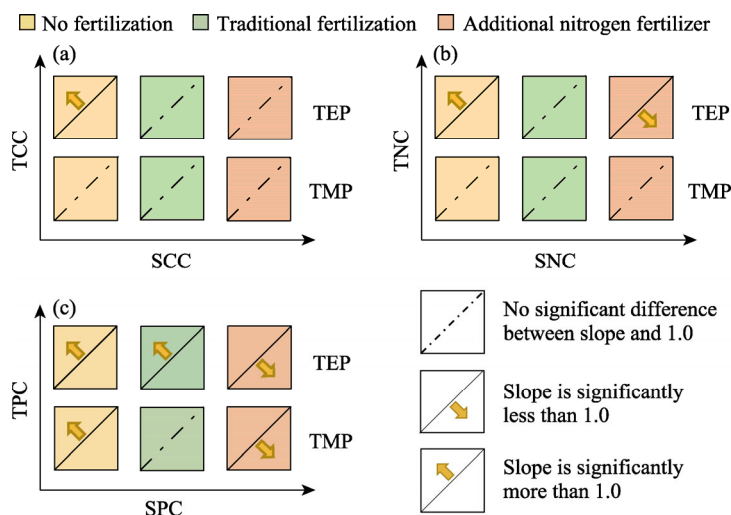


Fig. 5 Allometric relationship of nutrient elements content between stolon and tuber. (a), relationship between SCC (stolon carbon content) and TCC (tuber carbon content); (b), relationship between SNC (stolon nitrogen content) and TNC (tuber nitrogen content); (c), relationship between SPC (stolon phosphorus content) and TPC (tuber phosphorus content). TEP, tuber expanding period; TMP, tuber mature period.

3.4 Stoichiometric ratios of tiger nut

During the growth of tiger nut, C:N ratio of leaves and stolons increased while that of tubers decreased. C:N ratio of roots only increased under fertilization treatments (Fig. 6). N:P ratio in stolons decreased with the growth of tiger nut, while that in tubers did not change significantly under traditional fertilization and no fertilization, but increased significantly under additional N fertilizer (Fig. 6).

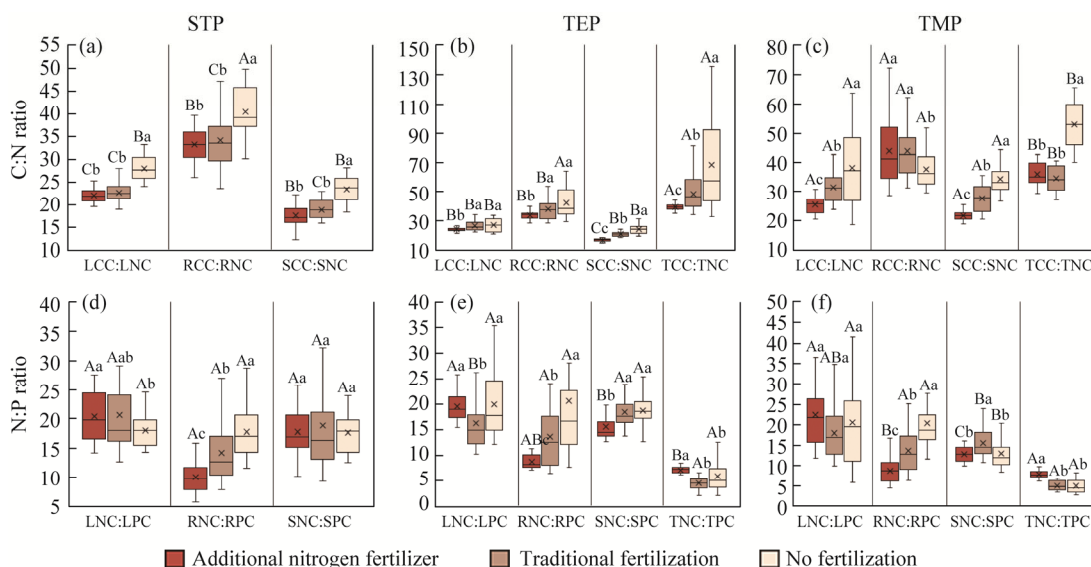


Fig. 6 C:N ratio (a–c) and N:P ratio (d–f) in tiger nut organs under different growth periods and treatments. Different lowercase letters within the same treatment indicate significant differences among different periods at $P<0.05$ level, while different lowercase letters within the same period indicate significant differences among different treatments at $P<0.05$ level. LCC, leaf carbon content; LNC, leaf nitrogen content; RCC, root carbon content; RNC, root nitrogen content; SCC, stolon carbon content; SNC, stolon nitrogen content; TCC, tuber carbon content; TNC, tuber nitrogen content; LPC, leaf phosphorus content; RPC, root phosphorus content; SPC, stolon phosphorus content; TPC, tuber phosphorus content. STP, stolon tillering period; TEP, tuber expanding period; TMP, tuber mature period.

Under no fertilization, C:N ratio of all organs in tiger nut was significantly higher than that under the other two treatments. Prior to tuber production, there was no significant difference in C:N ratio across various organs between traditional fertilization and additional N fertilizer. However, as the tubers began to expand, C:N ratio of different organs in tiger nut was higher under traditional fertilization compared with additional N fertilizer. After the tubers reached maturity, there was no significant difference in C:N ratio of tuber between traditional fertilization and additional N fertilizer. However, C:N ratio of the stolon remained higher under traditional fertilization than under additional N fertilizer. N:P ratio of roots under the three treatments was significantly different, with the highest under additional N fertilizer and the lowest under no fertilization. Furthermore, N:P ratio of tubers under additional N fertilizer was significantly higher than that under the other two treatments (Fig. 6).

3.5 Variations in rhizosphere soil nutrients

Variations of rhizosphere soil nutrients are shown in Figure 7. We observed insignificant variation in OMR during the growth of tiger nut under no fertilization treatment, while the other two treatments displayed a significant increase. As tiger nut grew, the difference in TNR among the three treatments gradually dwindled until it was no longer significant, and TPR showed the same variation. Available nutrients exhibited a significant decrease with tiger nut growth in all treatments, and the difference in available nutrient content of rhizosphere soil between each fertilization treatment and no fertilization treatment was extremely significant ($P < 0.001$, Fig. 7).

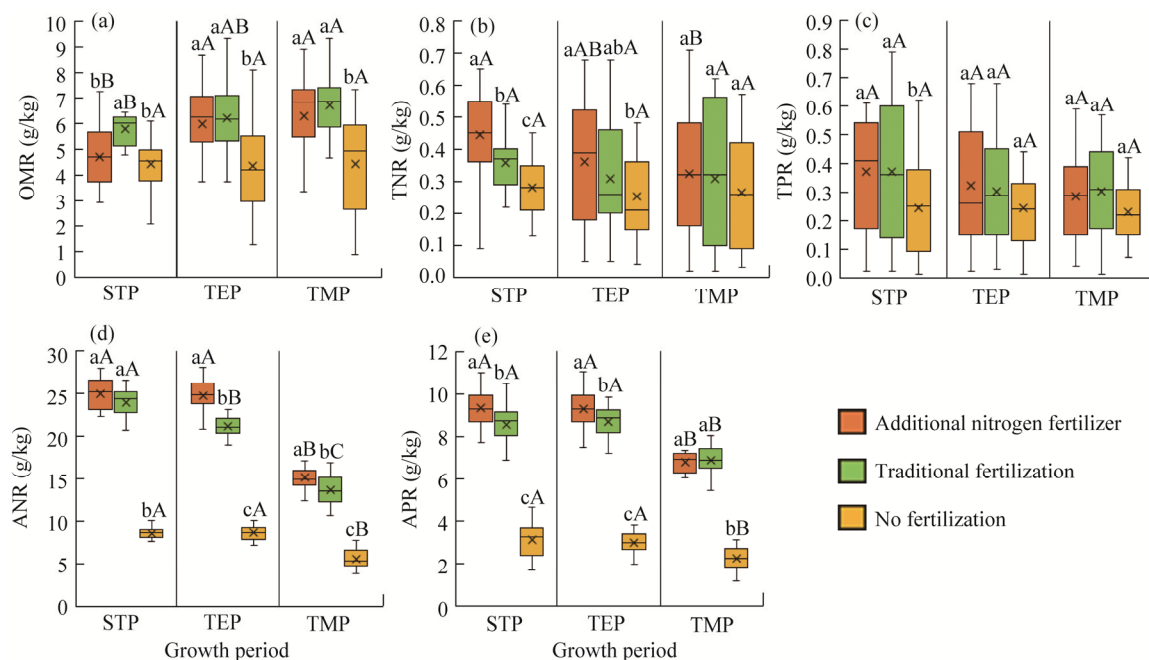


Fig. 7 Variations in rhizosphere soil nutrients under different treatments. (a), OMR (organic matter in rhizosphere soil); (b), TNR (total nitrogen in rhizosphere soil); (c), TPR (total phosphorus in rhizosphere soil); (d), ANR (available nitrogen in rhizosphere soil); (e), APR (available phosphorus in rhizosphere soil). Different lowercase letters within the same treatment indicate significant differences among different periods at $P < 0.05$ level, while different lowercase letters within the same period indicate significant differences among different treatments at $P < 0.05$ level. STP, stolon tillering period; TEP, tuber expanding period; TMP, tuber mature period.

3.6 Relationship between rhizosphere soil nutrients and stoichiometric characteristics

RDA results indicate that the explained variance of all rhizosphere soil nutrient types (including OMR, TNR, TPR, ANR, and APR) had the strongest correlation with the differences in stoichiometry in tiger nut across different treatments (Fig. 8).

The correlation analysis results indicate that, under additional N fertilizer, the N content in the

rhizosphere soil had a significant influence on LNC in STP. However, after tuber production, it had a significant influence on SNC. On the other hand, P content in the rhizosphere soil had a continuous influence on SPC throughout the growth cycle of tiger nut (Fig. 9). Under traditional fertilization, the availability of nutrients in the rhizosphere soil significantly influenced the corresponding element content of stolon before tuber production, but this influence shifted to the corresponding element content of tuber after tuber production (Fig. 9). Under no fertilization, both N and P contents in the rhizosphere soil had a significant influence on the corresponding element content of tuber after tuber production (Fig. 9). Moreover, OMR showed correlations with RCC and SCC under fertilization treatments in TMP (Fig. 9).

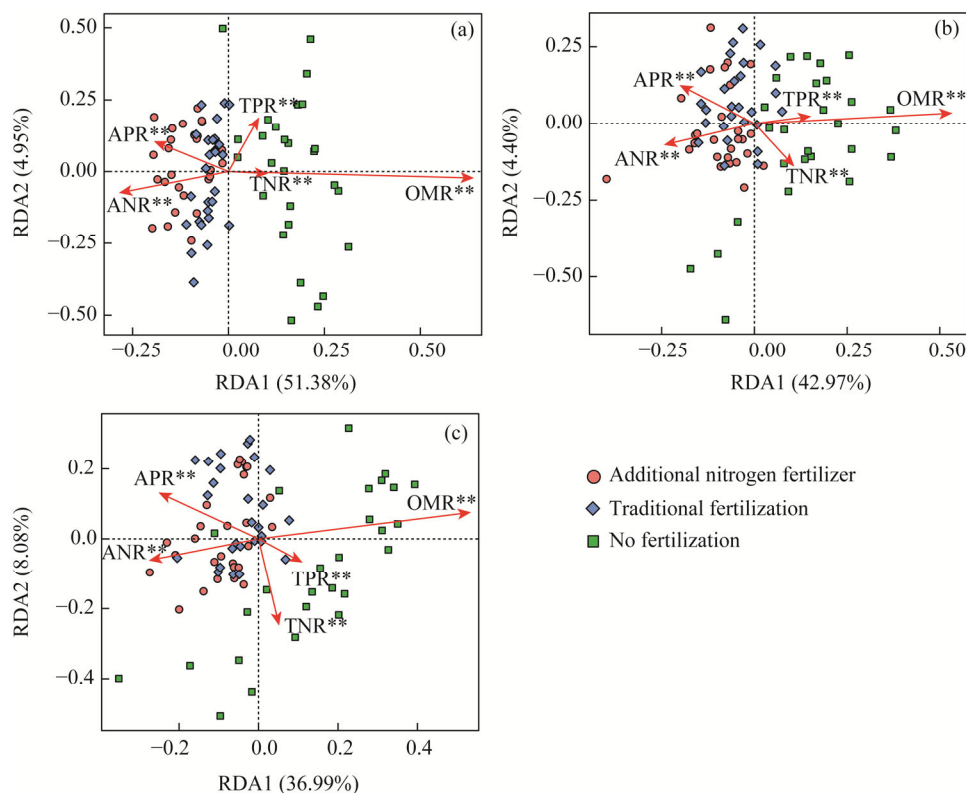


Fig. 8 Redundancy analysis (RDA) of stoichiometric characteristics of tiger nut and rhizosphere soil nutrients under different growth periods and treatments. (a), stolon tillering period; (b), tuber expanding period; (c), tuber mature period. ** indicates the rhizosphere soil nutrients were significantly correlated to stoichiometric characteristics of tiger nut under different treatments at $P < 0.01$ level. ANR, available nitrogen in rhizosphere soil; APR, available phosphorus in rhizosphere soil; TNR, total nitrogen in rhizosphere soil; TPR, total phosphorus in rhizosphere soil; OMR, organic matter in rhizosphere soil.

4 Discussion

4.1 Nutrient coordination mechanism of tiger nut under different treatments

Studies have shown that plants enhance their N utilization efficiency by increasing C:N ratio (Castellanos et al., 2018; Zhang et al., 2020). Moreover, the growth rate hypothesis suggests that organisms with higher growth rates require substantial ribosome and protein synthesis to sustain their growth, resulting in higher P content and lower N:P ratio in their cells. In contrast, slower-growing organisms tend to exhibit lower P content and higher N:P ratio (Elser et al., 1996; Tian et al., 2021). Based on these two theories, we attempt to explain the nutrient coordination mechanism of tiger nut caused by nutrient variations in rhizosphere soil.

Under no fertilization, N and P contents of tiger nut roots were influenced by their contents of

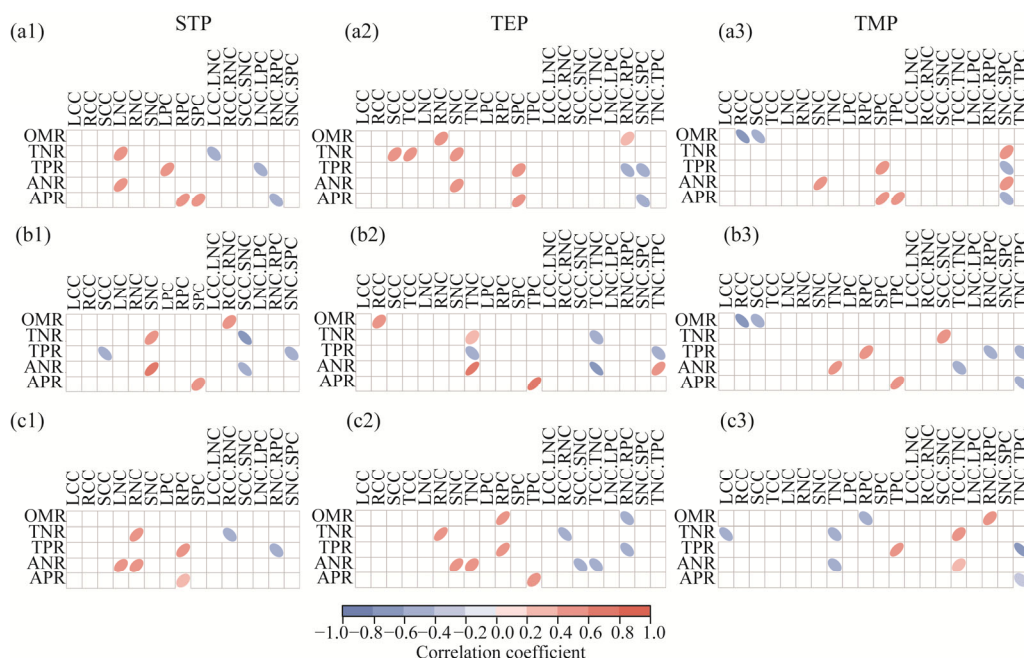


Fig. 9 Correlations between rhizosphere soil nutrients and stoichiometric characteristics of tiger nut. (a1–a3), additional N fertilizer; (b1–b3), traditional fertilization; (c1–c3), no fertilization. Only relationships with significant correlation ($P < 0.05$) were shown in the figure. OMR, organic matter in rhizosphere soil; TNR, total nitrogen in rhizosphere soil; TPR, total phosphorus in rhizosphere soil; ANR, available nitrogen in rhizosphere soil; APR, available phosphorus in rhizosphere soil; LCC, leaf carbon content; RCC, root carbon content; SCC, stolon carbon content; TCC, tuber carbon content; LNC, leaf nitrogen content; RNC, root nitrogen content; SNC, stolon nitrogen content; TNC, tuber nitrogen content; LPC, leaf phosphorus content; RPC, root phosphorus content; SPC, stolon phosphorus content; TPC, tuber phosphorus content; STP, stolon tillering period; TEP, tuber expanding period; TMP, tuber mature period.

the rhizosphere soil (Figs. 7 and 9). This resulted in tiger nuts allocating more carbon to the roots, leading to a high C:N ratio in the roots, which improved nutrient utilization efficiency in a limited environment (Figs. 4 and 6) (Zhang et al., 2020). However, N:P ratio of the roots was significantly higher than the other treatments, suggesting that root development was limited and resulting in a relatively insufficient supply of N and P to the leaf and stolon (Fig. 3). Nevertheless, tiger nut took timely remedial measures. When tubers were produced, the roots maintained a high C:N ratio to ensure efficient nutrient utilization (Fig. 6), and the root may also activate inorganic nutrients in the rhizosphere soil to facilitate nutrient acquisition (Fig. 9) (Badri and Vivanco, 2009). While the stolons and tubers maintained a high C:N ratio to maximize the utilization of the scarce nutrition obtained from the roots (Fig. 6). As the tubers mature, the available N content in the rhizosphere soil decreased due to consumption (Fig. 7), so the tubers continued to have high C:N ratio and low N:P ratio to optimize tuber quality (Figs. 6 and 9). Tiger nuts may utilize limited N to promptly form relatively stable cell walls in the tubers (Fig. 3) (Tian et al., 2022), promoting tuber structure stability and facilitating subsequent storage of P and other nutrients (Figs. 3 and 5). Therefore, it was evident that due to inadequate nutritional supply, tiger nut allocated energy to the tubers, ensuring the reproduction of their offspring in a limited environment. In such conditions, tuber development was constrained by rhizosphere soil nutrients, making it challenging to achieve optimal results, however, tiger nut made efforts to optimize tuber development as much as possible. The strong adaptability of tiger nut makes them an ideal pioneer crop for the reclamation of new marginal lands. If the goal is focused on improving the soil environment rather than maximizing yield, it may be crucial to provide few fertilizer application during the challenging early emergence (Table 1). This minimal intervention can assist tiger nut in overcoming initial obstacles and establish a strong foundation for subsequent

growth.

Under traditional fertilization, the allocation of nutrients in tiger nut did not favor either the leaves or the roots, indicating that the pressure on tiger nut to obtain nutrients has been alleviated after fertilization (Fig. 4). However, as the available N in the rhizosphere soil decreased (Fig. 7), the C:N ratio of leaf, root, and stolon gradually increased to fully utilize the decreasing amount of N in the soil (Figs. 6 and 7). Compared with no fertilization, the rapid accumulation of P in stolons appears to promote the production of more new shoots under traditional fertilization, although not as much as with additional N fertilizer (Fig. 4; Table 1), and the availability of P in the rhizosphere soil seemed to play a key role for this performance (Figs. 8 and 9). From the onset of tuber production, tubers became a primary target for P allocation and facilitated the stable transfer of nutrients to the tubers (Figs. 3 and 5). Throughout the tuber maturation process, the positive effects of rhizosphere soil nutrients on tuber nutrient levels persisted (Figs. 7 and 9), allowing the tubers to maintain a constant N:P ratio at a lower C:N ratio, ensuring their stable development (Fig. 6). Under traditional fertilization, tiger nut fully utilized the rhizosphere soil nutrients, ensuring stable development of vegetative organs while facilitating stable nutrient supply to the tubers during periods of soil nutrient depletion. This stable nutrient allocation strategy, which effectively utilizes and allocates resources, proves beneficial for crop growth (Viciedo et al., 2021).

Under additional N fertilizer, N content in the rhizosphere soil increased (Fig. 7), resulting in higher N levels in the leaves of tiger nut during early growth (Figs. 3 and 9). This appeared to enhance the photosynthetic capacity of the leaves and promote C accumulation (Fig. 3) (Park et al., 2019). During this period, there was no significant difference in N:P ratio of tiger nut stolons among the three treatments (Fig. 6). However, as tiger nut continued to grow under additional N fertilizer, more P accumulated in the stolons rather than in the tubers (Figs. 3 and 5), leading to a significant decrease in N:P ratio of the stolons (Fig. 6). This may have contributed to a faster growth rate of stolons. On the other hand, when tubers were produced, N accumulated in the stolons was transported to the tubers, while P seemed to have been utilized within the stolons (Fig. 5), resulting in an increased N:P ratio in the tubers (Fig. 6), potentially delaying tuber development (Dingenen et al., 2019; Li et al., 2021). Therefore, we speculated that in this particular soil environment, tiger nut did not primarily rely on slow nutrient transportation to the tubers as the main reproductive approach. Instead, they were compelled to adopt a reproductive strategy of producing new shoots through stolons at a faster growth rate. Additionally, the abundant underground tissues of tiger nut, including roots and stolons (Table 1), could contribute organic matter to the rhizosphere soil (Figs. 3, 6, 8, and 9) through degradation at the end of the growth cycle (Prescott et al., 2021), which was beneficial for nutrient-deficient marginal lands.

In summary, we present a concise description of the nutrient coordination mechanism of tiger nut (Fig. 10). The poorer the nutrients in the rhizosphere soil, the higher the C:N ratio of tiger nut, to optimize nutrient utilization in a limited environment, maintain a stable N:P ratio in the tubers, and ensure the development of progeny. The higher the nitrogen content in the rhizosphere soil, the lower the C:N ratio of tiger nut. N accumulated in the stolons requires greater P transport before tuber production, leading to a reduced N:P ratio in tubers with insufficient P, leading to the delayed development. But tiger nut is driven to produce more new shoots through the stolons.

Based on two different nutrient coordination modes observed in tiger nut under two fertilization treatments, we propose some recommendation for production of tiger nut. If the primary purpose is to maximize tuber production, we suggest using a fertilizer with N and P ratios as closely aligned as possible. An alternative approach would involve applying a fertilizer with a high N ratio in STP and supplementing with P fertilizer in TEP. This approach aims to address any potential depletion of P in the tubers (Fig. 3). By adopting these measures, tiger nut has the potential to promote the growth of more new shoots and enhance stable tuber production from new shoots, resulting in optimal tuber yield. If the primary purpose is to maximize aboveground biomass production, it is recommended to apply fertilizer with a high N ratio. This is particularly beneficial considering that the leaves of tiger nut can be utilized as high-quality forage (Edo et al.,

2023). Additionally, the abundant aboveground tissue provides effective sand fixation effects in arid areas (Gao et al., 2005).

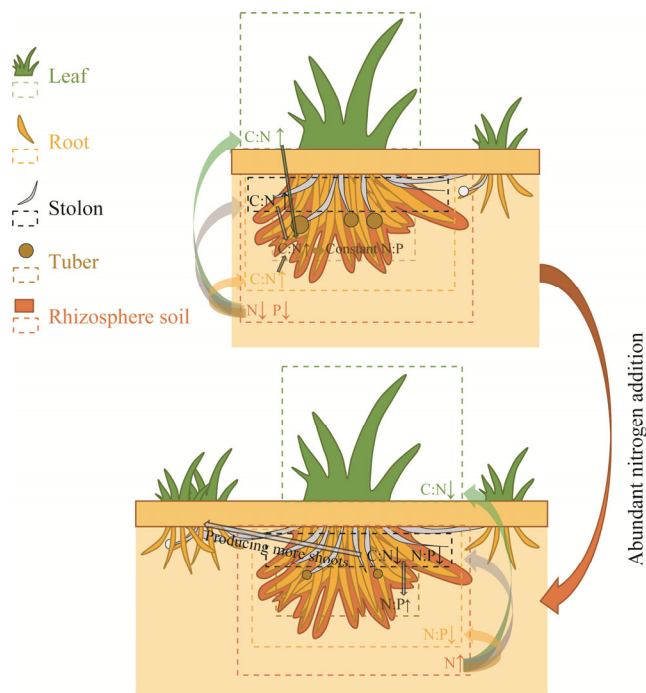


Fig. 10 Brief schematic diagram of nutrient coordination mechanism of tiger nut induced by rhizosphere soil nutrient variation

5 Conclusions

The scarcity of rhizosphere soil results in the nutrient of tiger nut being allocated for the purpose of enhancing nutrient absorption ability, and increasing their C:N ratio to enhance nutrient utilization efficiency, leading to tubers having a stable N:P ratio for their development. While the N levels in the rhizosphere soil rise significantly, C:N ratio of tiger nuts decreases. In this case, the stolons develop fully before tuber production, and low N:P ratio promotes rapid stolon growth, resulting in more new shoots being produced, while high N:P ratio delays the development of tubers. To achieve the maximum tuber yield, it is recommended to use a fertilizer with closely aligned N and P ratios, or apply a fertilizer with a high N ratio in stolon tillering period and then supplement with P fertilizer in tuber expansion period to meet the P requirements of the tuber. To maximize aboveground biomass, it is advised to use a fertilizer with a high N ratio.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author contributions

Conceptualization: TAN Jin, WU Xiuqin; Data curation: TAN Jin, WU Xiuqin; Formal analysis: TAN Jin; Writing - original draft preparation: TAN Jin; Writing - review and editing: TAN Jin, WU Xiuqin; Funding acquisition:

WU Xiuqin; Investigation: TAN Jin, LI Yaning, SHI Jieyu, LI Xu; Methodology: TAN Jin; Project administration: WU Xiuqin; Supervision: WU Xiuqin; Validation: WU Xiuqin, LI Yaning; Visualization: TAN Jin, SHI Jieyu, LI Xu.

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